

AN INVESTIGATION OF THE SOOTY MOULDS OF NEW SOUTH WALES. III.
THE LIFE HISTORIES AND SYSTEMATIC POSITIONS OF AITHALODERMA AND CAPNODIUM,
TOGETHER WITH DESCRIPTIONS OF NEW SPECIES.

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(Sixty-five Text-figures.)

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Introduction.

The systematic position of the Capnodiaceae has been the subject of investigation by several workers, but as yet no ontogenetic studies have been made, with the exception of that of Arnaud (1910) on *Pleosphaeria* (*Aithaloderma*) *citri*. Arnaud followed the early development of the young fruit body, but was unable to trace the formation of an archicarp.

Theissen and Sydow (1917) and the older systematic mycologists placed the Capnodiaceae in the Perisporiales with the Erysiphaceae and Perisporiaceae. Arnaud (1911), and later Gaumann (1928), considered that their affinities lay rather with the Sphaeriales because of the presence of an ostiole and the method of development of the perithecium. Von Hoehnel (1918) described the Capnodiaceae as having Pseudosphaerialean structure. Woronichin (1925) considered them sufficiently distinct to be raised to the rank of an order, the Capnodiales. Von Hoehnel (1910) considered that some of the fungi which were included by Theissen and Sydow in the Capnodiaceae should be placed in the Sphaeriales, and Petrak (1929) believed that the Chaetothyriaceae, recognized by Theissen and Sydow as a sub-section of the Capnodiaceae, comprised very heterogeneous elements, most of which were probably not closely related to the Capnodiaceae.

Arnaud's classification involves the inclusion of the species of the Capnodiaceae in already described genera of the Sphaeriales. Thus *Capnodium citri* became *Pleosphaeria*, and *C. salicinum* became *Teichospora*.

Any discussion of the nomenclature of these species must, therefore, be based on a consideration of their systematic position.

Very little is known about the development of the fruit body in the Capnodiaceae, most of the work having been done on mature fructifications. Arnaud described the formation of a stroma by the division of cells of a vegetative hypha to form a flat disc which, by further growth, becomes almost globular. He did not describe the early development of the archicarp, but recorded the growth of the young asci at the expense of the stroma.

For the present investigation, material was fixed in the field, the most satisfactory reagents being Flemming's weak fixative, and chromo-acetic 1% solution diluted with an equal volume of water. Sections cut at 4μ were stained with Haidenhain's iron-alum Haematoxylin. For confirmation sections 2μ thick were

stained with safranin and gentian violet, and by Newton's iodine-gentian violet method.

The life-histories of four fungi are considered in the following account. Three of these, *Capnodium salicinum* var. *uniseptatum*, *Aithaloderma ferruginea* and *A. viridis*, are here described as new and will be discussed in more detail in the succeeding papers of this series. The genus *Aithaloderma* is placed in the sub-section Chaetothyriaceae of the Capnodiaceae by Theissen and Sydow, *Capnodium* being the type genus of the sub-section Eucapnodiaceae.

CAPNODIUM SALICINUM VAR. UNISEPTATUM, n. var.

Mycelio epiphylo. Hyphis fuscis, dense ramosis anastomosisque. Cellulis elongatis vel breviter constrictis, $3.5-5 \times 5-12\mu$. Pycnidiis erectis, elongatis, $300-650\mu$ longis, ad basem $50-70\mu$ crassis, ad apicem $20-30\mu$ crassis. Apici fimbriata. Pycnidiosporis hyalinis, 1-septatis, ellipticis, prima nonconstrictis, $3.5-4.5 \times 7-8\mu$, dein constrictis $5 \times 8-9\mu$. Ascstromis globosis vel ellipticis, ad apicem obtusis, glabris, sessilibus vel saepe stipitatis, $80-120 \times 100-200\mu$. Ascis clavatis, ad basem attenuatis, $50-60 \times 15-20\mu$, octosporis. Ascosporis atrofuscis 3- vel raro 5-septatis, medio septo saepe constrictis, 1-4-longitudinaliter septatis, oblongis untrinque rotundatis, $17-22 \times 7-9\mu$.

Mycelium dark brown, dematioid, the cells $3.5-5 \times 5-12\mu$. Pycnidia elongate, $300-650\mu$ in length, $50-70\mu$ wide at the base, $20-30\mu$ wide at the apex. The apex is fringed by a ring of hyaline 1-2-celled, hair-like hyphae $20-30\mu$ long. Pycnidiospores hyaline, 1-septate, oval, $3.5-4.5 \times 7-8\mu$. Ascstromata globular or slightly vertically extended, shortly stalked, $80-120\mu$ wide by $100-200\mu$ long inclusive of the stalk. The stalk is $20-100\mu$ long. Asci are numerous, clavate, $50-60 \times 15-20\mu$, eight-spored. Ascospores are irregularly grouped in the ascus, greenish-brown, becoming dark brown when mature, with 3 or rarely 5 transverse septa, and a varying number of longitudinal septa, often two at right angles between each transverse septum. The mature ascospores are characteristically slightly constricted at the middle septum.

Type collection from Pennant Hills, on *Spartium* sp., 6, 1932.

AITHALODERMA FERRUGINEA, n. sp.

Mycelio epiphylo, late effuso, ex hyphis ramosis anastomosisque, plerumque longitudinaliter connatis, subfuscis, cellulis cylindricis, vix constrictis, $4-5 \times 5-8\mu$. Pycnidiis breviter conoideis, $85-120\mu$ diam., ostiolis setis divergentibus fimbriatis. Setis atrofuscis, opacis, $70-140\mu$. Pycnidiosporis hyalinis, continuis, ovoideis, $5-6 \times 3\mu$. Ascstromis breviter conoideis, $100-150\mu$ diam., $50-85\mu$ crassis, olivaceo-fuscis. Apice distincte ostiolato. Ostiolis setis elongatis, divergentibus opacis fimbriatis. Ascis oblongis vel cylindricis, $60-75 \times 10-15\mu$, octosporis. Ascosporis hyalinis, 5-7-septatis, ad septa constrictis, apice rotundatis, deorsum attenuatis, $25-28 \times 5-6\mu$.

The mycelium is thin, light brown, almost slimy, the cells are $4-5 \times 5-8\mu$, slightly constricted at the septa. The pycnidia are conical, $85-120\mu$ in diameter, the apical pore is encircled by 6-10 divergent dark brown setae $70-140\mu$ long, which are opaque or nearly so and taper to a rounded point. The pycnidiospores are hyaline, one-celled, ovoid, $5-6 \times 3\mu$. The ascstromata are conical, $100-150\mu$ in diameter, $50-85\mu$ high in the centre. The apical pore is surrounded by setae similar to those present on the pycnidia. The asci are cylindrical or oblong, $60-75 \times 10-15\mu$, eight-spored. The ascospores are hyaline, typically 5-septate, but

occasionally 6- or 7-septate, slightly constricted at the septa, oblong, rounded at both ends but often tapering slightly towards the base, $25-28 \times 5-6\mu$. The walls of the pycnidia and ascostromata are dull brownish-yellow by transmitted light, but by reflected light appear a bright golden-brown.

Type collection from Pennant Hills, on *Citrus* sp., 6, 1933.

AITHALODERMA VIRIDIS, n. sp.

Mycelio epiphylo, late effuso, ex hyphis ramosis anastomosisque plerumque longitudinaliter connatis, subfuscis. Cellulis cylindricis, ad septa vix constrictis, olivaceo-fuscis, septatis non manifestatis. Pycnidiiis 200μ diam., tenuis, 45μ crassis, hyphis radiantibus constatis, primo virido-fuscis, dein atris, mature apici incomposite fractis. Pycnidiosporis hyalinis, continuis, oblongis, $4-5 \times 1\mu$. ascostromis ex hyphis radiantibus constatis, primo virido-fuscis, dein atris, $150-200 \times 50-80\mu$. Ascis clavatis, ad apicem incrassatis, $50-70 \times 17-20\mu$, 4- vel 8-sporis. Ascosporis hyalinis, 4-septatis, constrictis, $24-26 \times 4-5\mu$.

The mycelium is thin, olive-brown, the cells are scarcely constricted at the septa, the transverse walls are not clearly distinguishable, the individual cells are $3.5-4.5 \times 10-17\mu$. The pycnidia average 200μ in diameter, and are rather thin, 45μ in height at the centre. When young the pycnidia resemble the fructifications of the Microthyriaceae, since they consist of a disc of closely-associated radiating hyphae. The pycnidiospores are hyaline, one-celled, $4-5 \times 1\mu$. The apex of the pycnidium splits by means of radiating cracks at maturity, and no setae are present around the apex. The ascostromata show the same radiating structure as the pycnidia. They are $180-200\mu$ in diameter by $50-80\mu$ in height. An apical pore is developed at maturity, but radiating cracks also appear as in the pycnidia, no setae are present around the apex. The asci are clavate, somewhat thickened at the apex, $50-70 \times 17-20\mu$, 8- or 4-spored. The ascospores are hyaline, 4-septate, somewhat constricted at the septa, $24-26 \times 4-5\mu$. The pycnidia and ascostromata are olive-green when young, and black at maturity with a radiating border of olive-green hyphae.

Type collection from Glenrock (Newcastle district), on *Elaeodendron australe* Vent., 8, 1933, coll. A. Burges.

The Life History of Aithaloderma ferruginea.

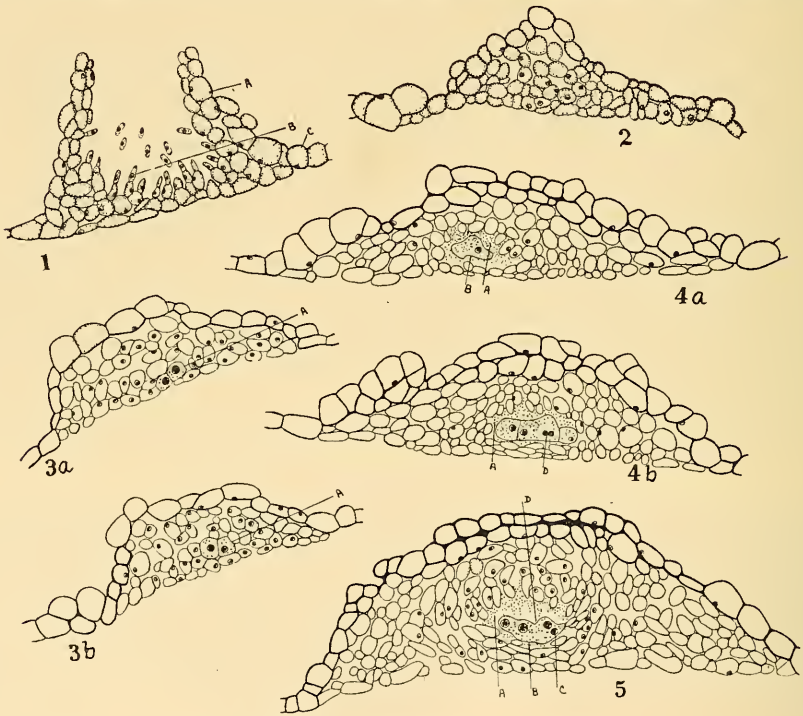
The mycelium of this species is brown and usually forms only a thin covering on the leaf. The hyphae, which consist of uninucleate cells, branch and anastomose at wide angles. The branching is in one plane only, parallel to the surface of the leaf, so that the mycelium forms a thin web over the surface.

The pycnidia arise on the young mycelium. Their development usually precedes the formation of ascostromata, but is very irregular and may not take place at all. They arise by the division of two or more adjoining cells of a hypha, frequently those of a branch joint or anastomosis, to form a thread of short wide cells. Further divisions give rise to a flat plate of cells. These cells then give rise to upward-growing hyphae which form a very short column which is further widened at the base by radial growth. The upward-growing hyphae form a wall layer of interwoven cells, leaving a central hollow area. Pycnidiospores are budded inwards into this hollow by the wall cells and the cells at the base of the young pycnidium. The mouth of the mature pycnidium is relatively wide and may be fringed by a few dark erect setae (Text-fig. 1).

The ascogenous fruits originate in a similar manner. A flat disc is formed by the lateral growth of hyphae originating by the segmentation of adjoining

cells of a hyphal thread, in the manner described for *A. citri* by Arnaud (1910). According to Arnaud, further growth in *A. citri* takes place under this flat disc. In *A. ferruginea* a certain amount of upward growth takes place also. After a brief period of upward growth, the uppermost cells of the disc differentiate out, becoming dark-walled and rigid (Text-fig. 2). The stroma then increases in size by the growth of hyphae beneath this covering. These hyphae become crowded and intertwined, and the centre of the disc becomes much thickened so that the stroma is finally hemispherical. Increase in diameter is effected by radial growth of hyphae around the margin of the disc. The young stroma therefore consists (Text-figs. 2-4) of a layer of dark-brown wall-cells, beneath which is a core-tissue of interwoven thin-walled hyphae, the base of which is in contact with the leaf on which the mould is growing.

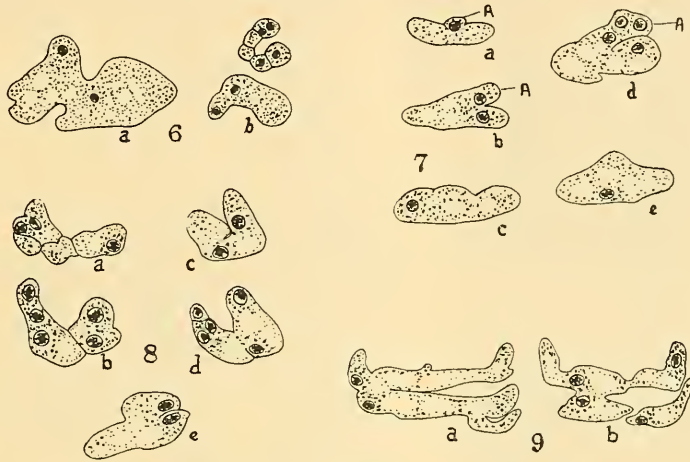
The archicarp arises in the core-tissue close to the base. In this species it can be distinguished from the core-tissue by the larger size of the cells, their



Figures 1-5. *Aithaloderma ferruginea*.

1.—Median longitudinal section of a mature pycnidium. A, wall; B, pycnidiospores; C, mycelium. 2.—Median longitudinal section of a young ascostroma, showing browning of the upper wall layer. 3.—Two successive median longitudinal sections of a young ascostroma, showing the development of the archicarp (A), part of which is shown in each of the sections. 4.—Two successive median longitudinal sections of a young ascostroma showing formation of multinucleate cell (B) and association of nuclei (D). A, mucilage. 5.—Median longitudinal section of an ascostroma showing increase in size of the archicarp (B) and the large size of the nuclei. A, mucilage; C, degenerating nucleus?; D, indentation in wall of archicarp showing probable position of resorbed wall. Figs. 1-5, $\times 700$.

greater tendency to hold stains and the size of their nuclei (Text-fig. 3, *a, b*). The number of cells which function as the archicarp could not be determined accurately, but appears to be four or more. The archicarp grows at the expense of the cells of the core-tissue surrounding it. These become disorganized and are resorbed. Very soon after increase in size commences in the archicarp, a deeply-staining layer of mucilaginous material becomes apparent around it. This is the unresorbed portion of the disorganized core-tissue, and it marks off the archicarp very sharply. The next stage in archicarp development is shown in Text-figure 4. The archicarp is seen to have enlarged considerably, and only two cell walls are visible in it. Though the process could not be observed in the material available, it seems certain that the walls between the archicarp cells break down and the nuclei are thus associated in one large cell. Certain indentations in the wall of the multinucleate archicarp (D in Text-fig. 5) indicate where septa probably



Figures 6-9. *Aithaloderma ferruginea*.

6.—Successive transverse sections of an archicarp showing branching; 6*b* shows the cut apices of vertical branches. 7, 8, 9.—Successive longitudinal sections of archicarps showing branching. Figs. 6-9, $\times 1,170$.

occurred. It is very unlikely that a multinucleate archicarp such as is shown in Text-figures 4 and 5 could be formed by the enlargement of one cell of the original archicarp, and division of nuclei in this, since no crushed archicarp cells were observed. Moreover, the entire archicarp is invested in a mucilaginous sheath and is clearly multicellular in the youngest stages.

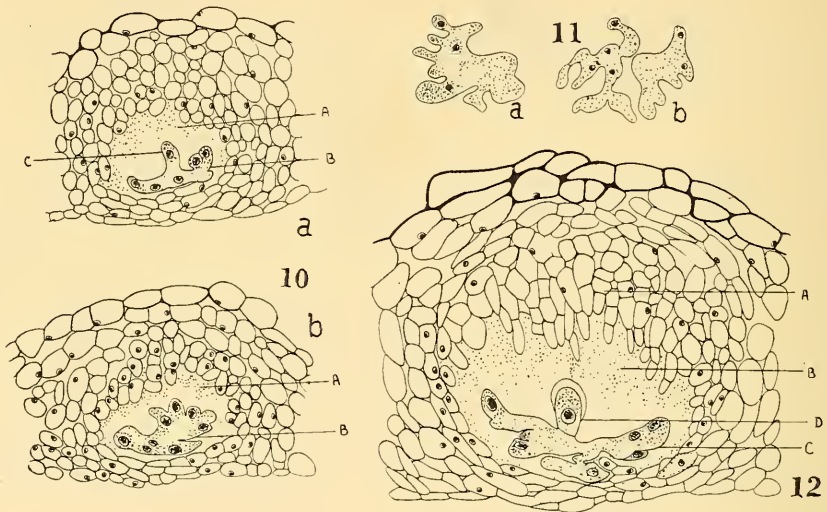
In the archicarp shown in Text-figure 4*b*, several septa appear to have been resorbed and one is still intact.

The writer considers it probable that the nuclei then fuse in pairs. Two nuclei are seen in close proximity in Text-figure 4*b* at D, and a similar condition has been observed in a number of other sections. (A few cases have been noted in which a pair of nuclei is in contact.) In Text-figure 5, which shows the archicarp at a slightly later stage, the nuclei are larger and fewer in number and the inference is that they are fusion nuclei.

Concurrently with the growth of the archicarp, the stroma has been increasing in size by means of hyphal growth and branching within the upper wall. There

is seen in section a tendency for the cells to be arranged in rows. This becomes very marked with further enlargement of the stroma and the rows develop definitely at right angles to the direction of growth of the ascogenous tissue (Text-figs. 10, 12). If the outer wall of the stroma breaks, which it does in places, due to the strain caused by the growing tissue below, the adjoining core-cells become brown and fill the gap. To cope with the internal growth which arches up the centre, further growth of the wall takes place in a radial direction around the edges, and further stromatic core-material is formed beneath this also, so that the radial as well as the vertical extent of the stroma is increased.

The archicarp nuclei then commence to divide. The actual process of division was not observed, and it is not known whether it is meiotic or mitotic in the first instance. The number of nuclei is considerably increased. At the same time the archicarp increases in size horizontally and a number of branches grow out from it. This is shown in surface section in Text-figure 6. Each of these out-



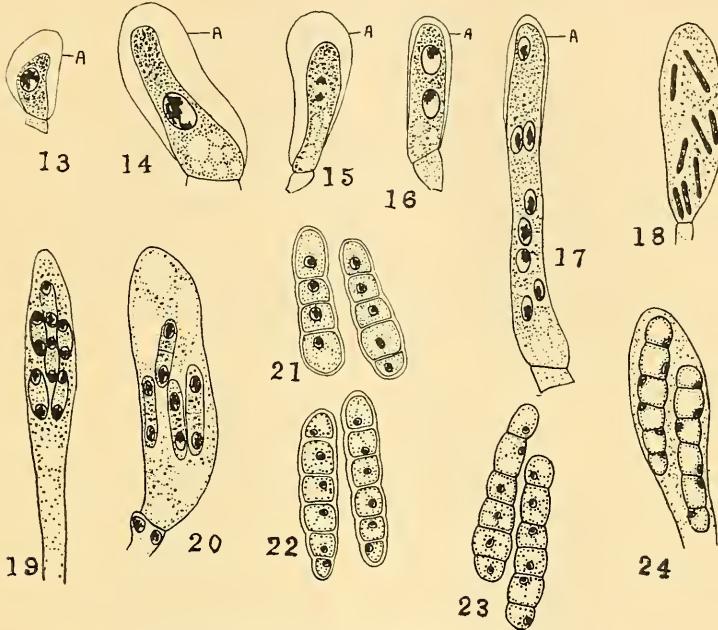
Figures 10-12. *Aithaloderma ferruginea*.

10.—Successive longitudinal sections of a developing ascostroma showing increase in size, and further branching of the archicarp. A, mucilage; B, ascogenous hyphae; C, young ascus. 11.—Successive transverse sections, *a*, lower, and *b*, upper, of developing ascogenous hyphae. 12.—Slightly oblique longitudinal section of a developing stroma to show the growth in strands of the stroma core tissue (A) around the ascogenous hyphae (C). B, mucilage; D, young ascus. Figs. 10-12, $\times 880$.

growths may branch repeatedly (Text-fig. 10) in all directions upwards and outwards. The further growth of these branches is chiefly horizontal. Text-figures 7 and 8 show stages in the early development of the branch system. The horizontal growth of the branches is shown in Text-figure 9, which shows an older stage in development, and in Text-figure 11, which shows the horizontal extent of the branch-system as seen in two successive surface sections. These branches, which arise from the archicarp and later give rise to the asci, are ascogenous hyphae. The number of nuclei in each branch is very variable, and

depends on the rapidity with which branching is taking place in relation to the rapidity of nuclear division in the branches.

Digestion of the overlying stroma cells continues concurrently with further growth of the stroma. Finally there results an almost globular fruit body, across the base of which is a complex branch-system of ascogenous hyphae, and the central part of which is occupied by the digested fragments of core-cells (Text-fig. 12). Early in the development of the ascogenous hyphal system, the asci commence to arise from the horizontal ascogenous hyphae as upgrowing branches which become cut off by a wall across the base (D, in Text-fig. 12). The young ascus is clearly distinguishable by its rounded shape and the large number of



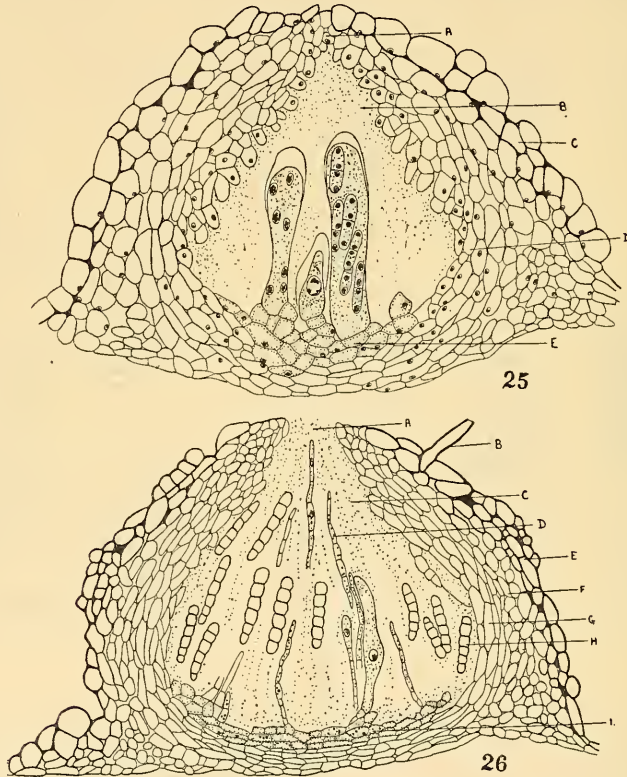
Figures 13-24. *Aithaloderma ferruginea*.

13, 14.—Young asci showing growth. A, mucilage cap. 15.—Ascus showing division of the nucleus. A, mucilage cap. 16.—Ascus showing binucleate stage, A, mucilage cap. 17.—Ascus showing 8-nucleate stage after increase in size of the nuclei. 18.—Ascus showing division of the eight nuclei. 19, 20.—Asci showing formation of ascospore walls. 21.—Young ascospores before the completion of the last division. 22.—Young ascospores showing thick hyaline walls. 23.—Ascospores showing contraction of walls. 24.—Mature ascospores. Figs. 13-24, $\times 1,170$.

densely-staining granules around the nucleus. As far as could be seen, only one nucleus enters the young ascus from the ascogenous hypha on which it arises, and no evidence has been obtained of nuclear fusion in it.

The young ascus is shown in Text-figures 13 and 14. The nucleus is large and the chromatin is usually aggregated in one mass to which a few loose threads are attached. This condition is strongly suggestive of synapsis. The resting nucleus is, however, of the karyosome type, in which most of the chromatin is aggregated in one mass, so that, in the absence of further stages in division, it is not possible to say with certainty whether the first division of the ascus nucleus

is meiotic or not. The small size of the vegetative and sexual nuclei increases the difficulty of such observations. Nuclear division appears to be intranuclear (Text-fig. 15). The ascus becomes successively two-nucleate (Text-fig. 16), four-nucleate, and eight-nucleate (Text-fig. 17). The eight nuclei then divide (Text-fig. 18). A cell wall forms around each pair of daughter nuclei (Text-fig. 19) and a cross wall is formed (Text-fig. 20). A small two-celled ascospore results. Each nucleus divides (Text-fig. 25) and two further cross walls cut the young spore into four cells (Text-fig. 21). The two end-cells then divide again, the



Figures 25-26. *Aithaloderma ferruginea*.

25.—Median longitudinal section of an ascostroma to show the process of resorption of the pore (A). B, mucilage; C, outer wall; D, inner part of stroma; E, probable extent of ascogenous cells. $\times 700$. 26.—Median longitudinal section of an old stroma. A, pore; B, seta; C, mucilage; D, paraphysis-like hypha; E, outer stroma wall; F, core tissue; G, partly resorbed core tissue; H, ascospore; I, probable extent of ascogenous cells. $\times 400$.

mature spore being five-septate (Text-fig. 22). The walls are at first thick and hyaline, the cells densely protoplasmic, and the nuclei more or less homogeneous (Text-fig. 22). As the spore matures, it contracts slightly, the walls become somewhat thinner but remain colourless (Text-fig. 23), and the nuclei contract somewhat and have a prominent central mass of chromatin. These nuclei often

finally come to lie against the cell wall and the protoplasm becomes vacuolate (Text-fig. 24).

As the stroma nears maturity, the apex becomes much thinner by resorption of the core-cells (Text-fig. 25) and finally a pore is formed, fringed by fragments of digested cells and those in the process of digestion (Text-fig. 26). At this stage it is difficult to distinguish the much-branched ascogenous hyphae at the base of the stroma from the stroma cells immediately below them, as they are in close contact, and all more or less collapsed.

Narrow multicellular paraphyses-like hyphae develop from the ascogenous layer as the stroma becomes old (Text-fig. 26). Double stromata may occur; cases have been seen in which two unrelated archicarps have arisen in the same stroma.

A number of setae surround the apex of the mature stroma. Spores are ejected by the swelling of mucilage in the stroma.

The Life History of Aithaloderma viridis.

Development is rather similar to that of *Aithaloderma ferruginea*, but is interesting in that it represents a further extension of the radial habit of growth which is seen to a certain extent in *A. ferruginea*.

An extensive radial flat plate is formed by the developing pycnidium before any growth in thickness occurs. Growth in thickness, when it takes place, is practically all under this covering, the apex of which is broken by the pressure of the developing spores.

The ascostroma also forms a flat plate of radiating cells of considerable extent before growth in thickness takes place and, as in the case of the pycnidia, further growth is localized below the first-formed disc of cells. The radial growth continues as the stroma increases in thickness, to a much greater extent than in *A. ferruginea*, so that in surface view the ascostroma is seen to have a border of radiating hyphae which grow out for a short distance all round it.

As the ascogenous hyphae develop, digestion of core-tissue proceeds as in *A. ferruginea*. The stroma tissue around the ascogenous hyphae, by continued growth, forms a definite wall which stands out from the outer loosely-woven stroma tissue by its compactness (E, in Text-fig. 27). In old stromata this zone has all the appearance of a perithecial wall. The upper wall layer of the stroma is unable to extend to accommodate this increase, and breaks therefore occur at the apex. These expose part of the outer core-tissue, which becomes in consequence much browned (A, in Text-fig. 27). As in *A. ferruginea*, an apical pore develops by resorption (Text-figs. 28 and 29). The wall surrounding the developing asci becomes much thinner at maturity, due to continued resorption.

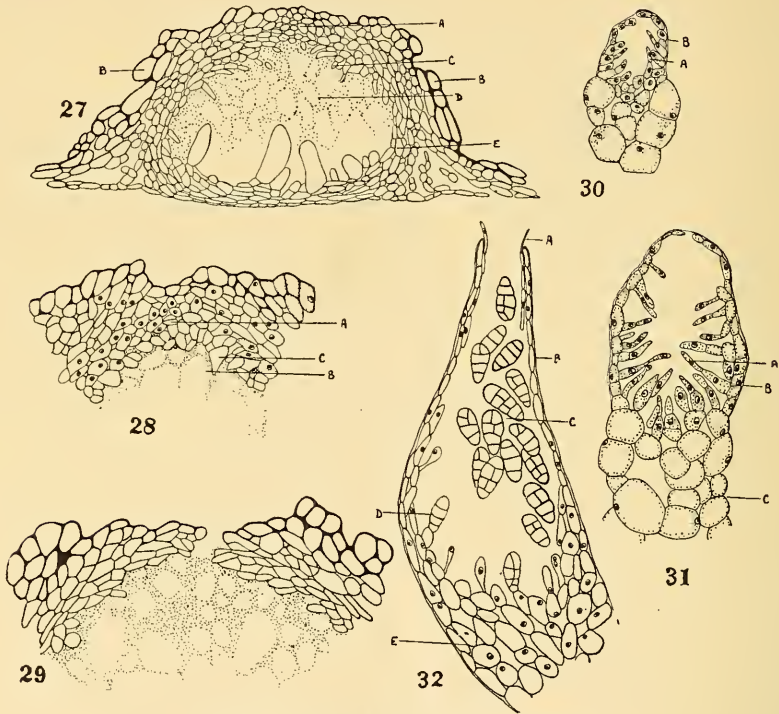
It is not uncommon to find two or more archicarps developing in the one stroma.

The Life History of Capnodium salicinum Mont.

The mycelium of *C. salicinum* consists of hyphae which branch and anastomose at wide angles in three dimensions to form a felt-like mass. The cells are brown-walled and uninucleate, the nucleus usually lying against the cell wall. There is a large central vacuole in the mature cell, and oil drops which were identified by their characteristic staining reactions, are frequently present.

Pycnidia arise on the young mycelium. The first indication is the division of two or more adjoining cells of a hypha, not infrequently those of a branch-joint or anastomosis, to form a thread of short wide cells. Further divisions give rise to a flat plate of cells whose walls are not so dark as those of the surrounding

mycelium. Cell walls are formed in all directions, and the cells round off slightly so that further divisions in these at right angles to their upper surfaces give rise to short filaments of cells. Only the upper cells of the plate are involved in this growth so that there results a short fascicle of upward-growing hyphae which are held close together by mucilage. The origin of the pycnidium is therefore compound meristogenous (Kempton, 1919). The basal cells of the fascicle enlarge and vacuolate, and become dark brown, thus forming a longer or shorter stalk. The hyphae of the stalk may branch, resulting in an increase in width. A certain amount of radial growth from the cells at the base of the stalk into the surrounding mycelium may also take place.



Figures 27-29. *Aithaloderma viridis*.

27.—Median longitudinal section of a young stroma showing the beginnings of the wall-like layer of the stroma tissue (E) round the young asci. A, stroma tissue which has broken through the upper wall layer (B). C, partly digested cells of the stroma; D, mucilage. $\times 400$. 28, 29.—Development of the apical pore by resorption. A, growing hyphae; B, mucilage; C, partly digested cells. $\times 700$.

Figures 30-32. *Capnodium salicinum*.

30.—Median longitudinal section of a very young pycnidium. A, young pycnidiospore; B, mucilage sheath. $\times 700$. 31.—Median longitudinal section of a young pycnidium. A, young pycnidiospore; B, mucilage sheath; C, stalk. $\times 700$. 32.—Median longitudinal section of a mature pycnidium. A, fringe of hairs; B, neck of pycnidium; C, detached spores; D, young spore; E, part of stalk. $\times 400$.

Further growth of the hyphae at the head of the stalk results in the formation of a wall layer 1-2 cells in thickness, and from these pycnidiospores are budded

off into the centre of the structure (Text-fig. 30). The wall-forming hyphae may be irregularly interwoven. The tips of the growing wall hyphae bend over so that the young pycnidium is almost enclosed. The wall hyphae continue their apical growth and further young pycnidiospores are formed, resulting in an irregular hymenial layer of growing spores which extends up the sides of the pycnidium (Text-fig. 31). The spores are not abstricted at this stage, but continue to increase in size. The mature pycnidium is shown in section in Text-figure 32. It is erect, standing well above the mycelium, and the apex is open and fringed with a row of hyaline hair-like cells which grow out from the inner wall layer.



Figures 33-38. *Capnodium salicinum*.

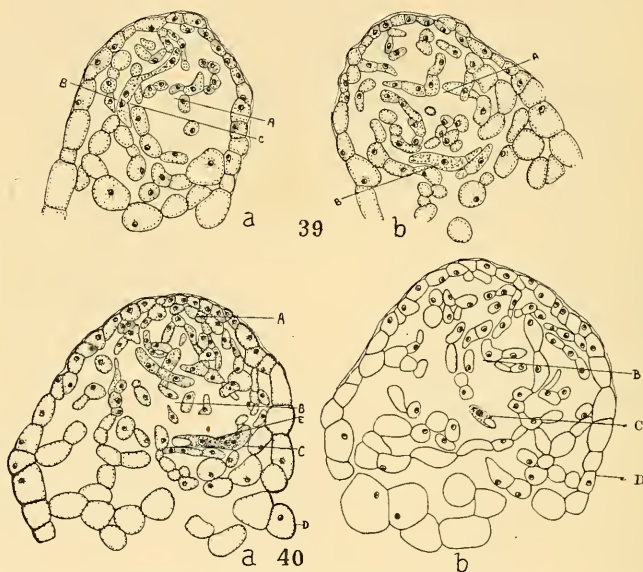
33, 34.—Median longitudinal sections of a very young stroma. A, mucilage sheath; B, young hyphae. 35-38.—Median longitudinal sections of developing stromata showing formation of a stalk. A, mucilage sheath; B, growing hyphae; C, stalk; D, mycelium; E, core tissue. Figs. 33-38, $\times 700$.

There are a number of spores lying free in the centre, which are typically brown-walled, three-septate, with or without additional longitudinal septa. Other spores are in the process of being budded off from the cells at the sides and base of the pycnidium. It is not known whether or not the same hymenial cell can bud off more than one spore, no chains of spores having been observed.

A considerable amount of mucilage is present in the mature pycnidium. This aids in spore dispersal by swelling with imbibition of moisture, thus bulging out through the neck and carrying detached spores.

The ascogenous fruits are produced at a later stage than the pycnidia. Young ones may be seen when pycnidial activity is at its maximum, but when they are mature few pycnidia are to be seen as a rule.

The early development resembles that of the pycnidium, a young stroma originating by the division of adjoining cells of a mycelial thread. A fascicle of upgrowing threads is formed (Text-fig. 33), but, unlike the young pycnidia, the hyphae form a more or less solid mass of intertwined cells. At first there is no differentiation into wall and inner cells, and hyphae twist indiscriminately about each other. The whole structure is invested in a mucilaginous sheath (Text-fig. 34). Further extension is by the apical growth and occasional branching of these cells. The older cells differentiate out behind the growing point, increase in size, become brown and vacuolated, and form a stalk of loosely-woven threads (Text-figs. 35-37).



Figures 39-40. *Capnodium saticinum*.

39.—Two successive median longitudinal sections of a young stroma showing the development of the archicarp, which is shown at B in both sections. A, core tissue; C, indentation marking probable position of resorbed cell wall. $\times 700$. 40.—Two successive longitudinal sections of a young stroma. The archicarp shows the association of 5 nuclei, 4 of which are shown in 40a and 1 in 40b. A, growing point of the stroma; B, core; C, archicarp; D, wall; E, probable position of resorbed cell wall. $\times 700$.

According to the growth of the apex, this stalk may be narrow (Text-fig. 36) or stout (Text-fig. 37), and may be long or so short as to be almost non-existent.

The growing point widens out considerably (Text-figs. 36-38), and soon a definite structure is visible in the young stroma, the stalk, a moderately well-defined wall of young growing cells, and a core of thin-walled densely protoplasmic hyphae which pass back into the brown-walled tissue of the stalk (Text-figs. 36, 37). This thin-walled area increases in extent, hyphal growth causing coiling within the sheath of the wall. Occasionally hyphae from the core may penetrate outside the wall and become wall elements (Text-fig. 37). Finally, as the stroma matures,

the cells of the core enlarge somewhat and become more vacuolate, but their walls remain thin and light in colour (Text-fig. 38). Growth continues at a slower rate at the apex. The core-cells contain considerable amounts of oil, identified by its characteristic staining properties, in the form of small droplets.

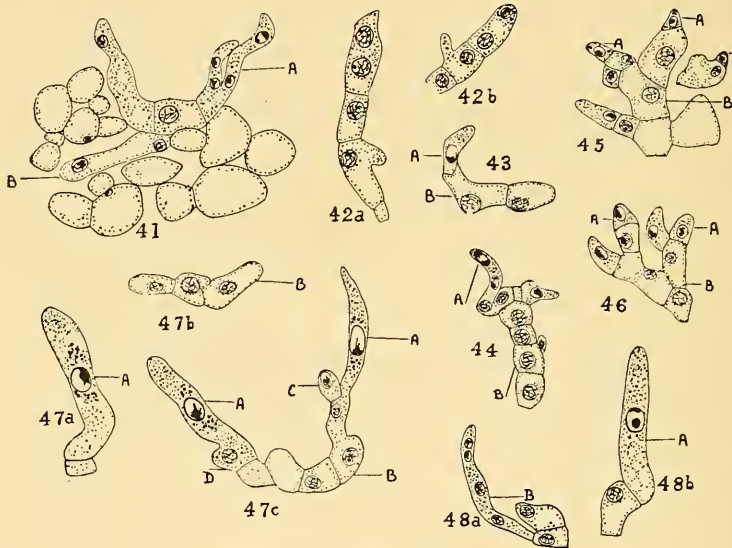
The time at which the archicarp appears is variable and does not altogether depend on the size of the stroma which may attain considerable dimensions before its appearance (e.g. Text-fig. 38).

The initiation of the archicarp is more obscure than in *Aithaloderma*, since a conspicuous layer of mucilage is not formed in the early stages of development. The first appearance is shown in Text-figure 39, *a* and *b*. An archicarp is visible at the base of the core at B, in which two nuclei are associated in the one cell. A distal cell with one nucleus is visible. In Text-figure 40, *a* and *b*, a later stage is shown. The young archicarp (C) is 5-nucleate and unicellular.

Since no stages in the actual breakdown of walls in the archicarp have been seen, it is impossible to say definitely that the multinucleate condition is not due to nuclear division and enlargement of one cell. Slight constrictions in the walls of the multinucleate archicarp, such as are shown at C in Text-figure 39 and at E in Text-figure 40, lend support to the idea that the multinucleate condition of the archicarp originates by the breaking down of cross walls in a filament of cells, and that these constrictions mark the original position of the cell walls. The shape of the archicarp which is invariably long and narrow further supports this view. Moreover, the nuclei are rather larger than those of the surrounding cells, and do not decrease in size with increase of numbers (compare Text-figs. 39 and 40) as, for instance, do the dividing nuclei in the developing ascus. The stages immediately following this nuclear association could not be followed in this species. It is suggested that they fuse in pairs since, in the next stage of development which has been observed, the nuclei are greatly enlarged (B, Text-fig. 41). One or more branches then grow out from the archicarp through the tissue at the base of the stroma core (Text-fig. 41). The nuclei divide, and cross walls are formed so that short filaments of three to four cells result (Text-fig. 42), the cells being uninucleate or occasionally binucleate by the non-formation of a wall. Several such hyphae may grow out from the archicarp, and in some cases their connection may be traced with a cell which is probably the archicarp, now empty and collapsed. After this stage the archicarp becomes entirely crushed out and cannot be detected with certainty. The nuclei of these ascogenous hyphae are many times larger than the surrounding vegetative nuclei, and the original archicarp nuclei. The chromatin is evenly distributed throughout them (Text-fig. 42). The cells of the ascogenous hyphae give rise to branches which may at once grow up as asci (A, Text-fig. 43). There are probably always one or two such primary asci in a stroma. Usually, however, the branches grow horizontally, further extending the range of the ascogenous tissue across the whole of the base of the stroma core (Text-figs. 44, 48, 49). Wall formation in these secondary ascogenous hyphae is not so regular as in the primary ascogenous hyphae, often no walls being formed except across the base of the young asci. Asci are produced at intervals by these hyphae and grow vertically upwards through the core of the stroma (Text-figs. 45 and 46). As far as could be seen, they each receive only one nucleus, and no evidence of fusion in the young ascus was obtained. As a general rule the ascus is cut off from the ascogenous hypha by a wall at an early stage. Cases have been observed, however, in which no wall had been formed and the base

of the ascus had budded out a further ascogenous hypha or an ascus (Text-fig. 47, D). Even when a wall is formed, young asci or ascogenous hyphae frequently grow out from immediately below it (C in Text-fig. 47c, and F in Text-fig. 49c). In a young stroma, therefore, asci are found in all stages of development (Text-fig. 49).

The young asci increase very much in size at the expense of the tissue they invade. A cap of mucilage soon becomes apparent over the top of the larger asci (Text-fig. 49). The early development of the ascus is shown in Text-figures 45 to 49. It is at first densely protoplasmic with numerous deeply-staining granules in the cytoplasm surrounding the nucleus. The nucleus increases in size, finally becoming very large. The chromatin is aggregated into one mass, usually towards



Figures 41-48. *Capnodium salicinum*.

41.—The development of the ascogenous hyphae (A) from the archicarp (B). 42.—Primary ascogenous hyphae showing septation and large size of nuclei. 43.—A young ascus (A) arising from a primary ascogenous hypha (B). 44.—A secondary ascogenous hypha (A) arising from a primary one (B). 45, 46.—Young asci (A) arising from ascogenous hyphae (B). 47a, b, c.—The development of asci from ascogenous hyphae as seen in three successive sections. A, asci; B, ascogenous hyphae; C, young ascus growing out from below an earlier formed one. 48a, 48b.—The development of asci (A) and an ascogenous hypha (B) from a primary ascogenous hypha, as seen in two successive longitudinal sections. Figs. 41-48, $\times 880$.

one end of the nucleus, and fine chromatin threads can sometimes be detected attached to it (Text-figs. 47 and 49). At times it has very much the appearance of a nucleus at the stage of synapsis, but, since the resting nuclei are of the karyosome type, it is impossible to say with certainty whether the first division of the ascus nucleus is meiotic or mitotic.

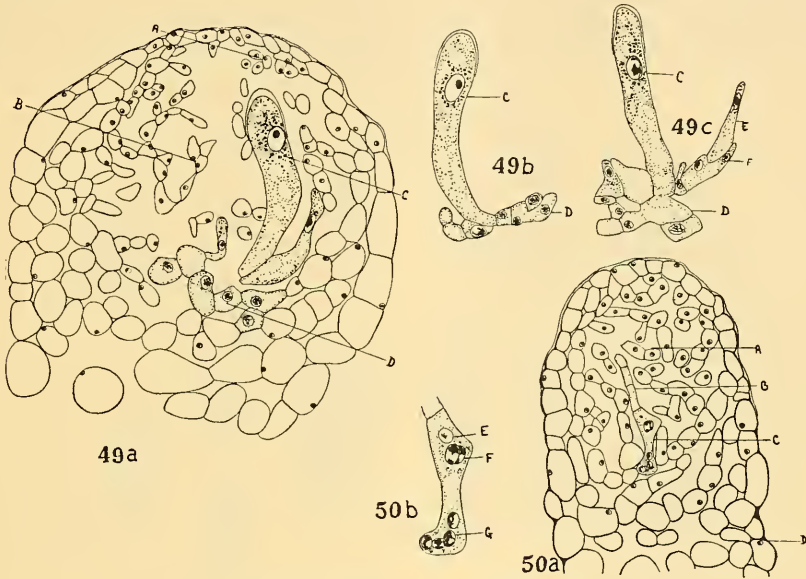
During the extension of the ascogenous hyphae and the development of the young asci, the stroma has continued its apical growth and the wall and outer core hyphae also increase by intercalary growth. A globular or slightly

elongated loculus results, which is usually of considerably greater diameter than the stalk. The central cells of the stroma are completely resorbed by the asci so that none remains between them.

Further development of the stroma and asci have been followed in a closely related variety *Capnodium salicinum* var. *uniseptum*.

The Life History of Capnodium salicinum var. *uniseptum*.

This variety differs from the type in that the pycnidia are frequently larger and more often branched; the pycnidiospores are smaller, uniseptate and hyaline, becoming brown when old if not ejected; and the ascostroma which, though of



49a, b, c. *Capnodium salicinum*.

The development of asci from ascogenous hyphae as seen in three successive sections. This also shows the development of the young stroma. A, growing point of the stroma; B, core of the stroma; C, asci; D, ascogenous hyphae. $\times 700$.

50. *Capnodium salicinum* var. *uniseptatum*.

50a.—Median longitudinal section of a young stroma showing the development of the archicarp. A, core; B, distal part of archicarp hypha; C, archicarp; D, stalk. $\times 700$. 50b.—The archicarp shown in Text-fig. 50a showing greater detail. E, degenerating nucleus?; F, two associated nuclei; G, four associated nuclei. $\times 1,500$.

similar size and appearance, has a slightly more compact stalk and more closely woven core. The ascospores are identical in the two varieties. Pycnidium formation and ascostroma formation are the same as in *C. salicinum*.

The archicarp is differentiated in the same way from a vegetative hypha at the base of the core tissue (Text-fig. 50a). The distal part evidently does not function, but later collapses. The archicarp is multinucleate, as in *Capnodium salicinum* (Text-fig. 40b), and a constriction at the centre may indicate the original position of a cross wall which has been resorbed. Two nuclei are shown in close contact at F in Text-figure 50b, but no cases of actual fusion have been

observed. At E in Text-figure 50*b* a nucleus appears to be degenerating. As in *Capnodium salicinum*, ascogenous hyphae bud out and grow across the base of the core, sending up young asci into the core tissue. An extreme case of branching at the base of an ascus is shown in Text-figure 51. The stroma continues to enlarge, and the cells surrounding the old archicarp darken, forming an almost solid base for the core and developing asci.

As in *Capnodium salicinum* the young ascus is densely protoplasmic, with a number of deeply-staining granules around the nucleus. The chromatin is aggregated into one large mass in the nucleus, as in the previous type. Prior to division, the chromatin becomes more evenly scattered (Text-fig. 52). The daughter nuclei of the first division are smaller, and retain the even distribution of the chromatin (Text-fig. 53). These divide again to give four still smaller nuclei (Text-fig. 54), and again to give eight, small, rather elongated nuclei



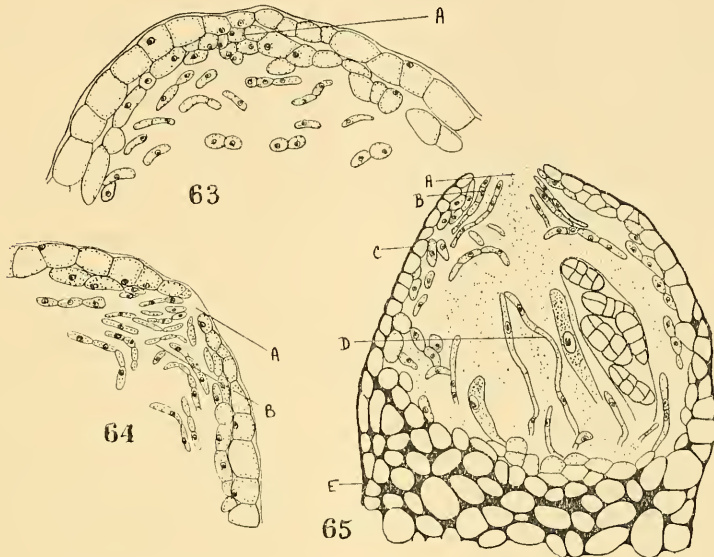
Figures 51-62. *Capnodium salicinum* var. *uniseptatum*.

51.—Young asci showing branching. 52-60.—The development of the ascus: 52, the ascus prior to the first division; 53, the binucleate stage; 54, the ascus showing 4 daughter nuclei; 55, the ascus at the 8-nucleate stage, 5 nuclei showing; 56, 57, the enlargement of the nuclei at the 8-nucleate stage; 58, wall formation round the young ascospores; 59, 60, divisions in the young ascospore. 61.—The mature ascospore. 62.—Mature ascospores shown in cross section to show the position of the vertical walls. Figs. 51-62, $\times 880$.

(Text-fig. 55). These eight nuclei increase in size considerably before undergoing further division (Text-fig. 56 and 57). They then divide and a wall is formed around each pair of nuclei with a cross wall between (Text-fig. 58), thus delimiting the young ascospores. The young ascospores increase in size and the nuclei divide twice (Text-figs. 59, 60). A cross wall is formed in each cell. Further nuclear divisions and longitudinal wall formation may occur. The walls of the young spores are hyaline. As the spore matures the walls become brown and rather thick (Text-figs. 61, 62). The nuclei contract slightly, and in the resting condition have a central mass of chromatin with very few free threads. So far as could be determined the divisions were intranuclear.

The stroma continues to increase in size to accommodate the developing asci. The core tissue becomes entirely resorbed, except for a thin layer lining the wall. The wall cells finally become very dark brown and thick-walled.

The development of an apical pore commences as the ascospores mature. The wall at the apex of the stroma becomes thinner than elsewhere, due to the effects of strain and resorption which are most concentrated at that point (Text-fig. 63). Ultimately, in spite of continued intercalary growth the cells are parted. While this process is going on, hyphae of the outer core tissue grow up under the pore from the sides (Text-figs. 63, 64) and simulate periphyses. The opening is made wider by the passage of spores (Text-fig. 65).



Figures 63-65.—*Capnodium salicinum* var. *uniseptatum*.

63.—Longitudinal section through the apex of the young stroma showing growing point (A). $\times 880$. 64.—Longitudinal section through the apex of the stroma showing the formation of a pore (A) and the growth of pseudoperiphyses (B). $\times 880$. 65.—Median longitudinal section of an old stroma. A, pore; B, pseudoperiphyses; C, outer wall; D, paraphysis-like hyphae; E, stalk. $\times 495$.

Finally, all peripheral core tissue and the pseudoperiphyses are resorbed, and further development of the asci is prevented by lack of available food material. The asci which commence development at this late stage appear to disintegrate without completing their growth. Towards the end of the life of the stroma, long, narrow, multicellular, paraphysis-like hyphae arise from the ascogenous layer at the base of the core (Text-fig. 65, D).

Bifurcating stromata are not uncommon, due to the development of two archicarps independently in the one stroma, all degrees of separation having been found. Stromata are also frequently developed from the sides of old pycnidia.

The Relationships of Capnodium and Aithaloderma.

A study of the development of these four fungi shows that there is a real relationship between them.

The mycelium is similar in the method of branching and anastomosing, and in the uninucleate condition of the cells.

The origin of the pycnidia is in all cases compound meristogenous, and a developmental series can be traced from *Capnodium*, in which the growth is upwards with a certain amount of radial and intercalary growth at the base, through *Aithaloderma ferruginea*, in which growth is chiefly radial, but some upward growth takes place, to *A. viridis* which shows the extreme development of the radial growth type. All agree in the formation of a vegetative stroma in which an archicarp arises, but differ in the method of growth of the stroma. In *Capnodium*, growth causes an extension in length and an increased diameter by means of an apical localized growing-point. In *Aithaloderma viridis* there is no localized growing-point, the bulk of the growth taking place under a cover layer, and radially around the edges of the stroma. *Aithaloderma ferruginea* shows how these two growth types may be related, since in the early stages of development of the stroma a certain amount of upward growth takes place.

The development of the archicarp from a vegetative hypha appears to be similar in *Capnodium* and *Aithaloderma ferruginea*, as far as could be ascertained. The subsequent development of ascogenous hyphae in the two genera appears to differ chiefly in the greater degree of septation shown in *Capnodium*.

The growth of the young asci, the development of ascogenous hyphae from below the young ascus, and the continued formation of asci are identical in all types.

In all the species the development of the pore is by the digestion of the apical cells of the stroma wall. Growth of stromatal core hyphae to form pseudo-periphyses is marked in *Capnodium salicinum* var. *uniseptatum*, but does not occur in *Aithaloderma*.

A series can be traced in the development of a special wall around the asci. In *Capnodium* this does not occur, and the outer wall layer of the stroma, after the resorption of the core cells, serves as a wall for the mature ascospores. In *Aithaloderma ferruginea* the stromatal core is much more compact and wall-like, and by its method of growth forms a wall around the developing asci, but is not abruptly differentiated from the rest of the stroma. In *A. viridis* this layer is separated from the outer wall of the stroma at the base by much looser tissue, and stands out very conspicuously.

Von Hoehnel (1910) considers that the genus *Limacinula* is distinct from the Capnodiaceae, where it was placed by Theissen and Sydow, and describes the presence of a true perithecial wall more or less embedded in stromatal tissue. It is possible that this so-called perithecial wall may be a development of stroma tissue such as is described in *Aithaloderma viridis*.

The Relationships of the Family Capnodiaceae.

In considering the relationships of the family the nature of the ascospore-producing fruit-body must first be considered. Though reduced to a single loculus and resembling a typical perithecium when mature, developmentally it is a stroma—a stroma which continues to grow after the archicarp is initiated, and which may develop a stalk and a wall within itself.

The bearing of these observations on the systematic position of the family is here briefly discussed. The difference between the stromatic Sphaeriales and the Dothideales lies in the fact that a perithecial wall is developed around the ascogenous tissue within the stroma of the former, but in the latter no wall is

formed and the asci develop simply in locules in the stroma. In 1907 a new family, the Pseudosphaeriaceae, was described by von Hoehnel for certain species previously placed in the Sphaeriaceae. These fungi were considered to be intermediate in character between the stromatic Sphaeriales and the Dothideales. Their perithecia were considered to be unilocular stromata. No developmental studies were made, however, and all his conclusions were based on an examination of mature or nearly mature fructifications. The family was greatly enlarged by further additions from the Sphaeriales by von Hoehnel and Theissen, and in 1918 Theissen and Sydow raised them to the position of an order, the Pseudosphaeriales. Petrak (1923), in a comprehensive study of the group and its related species, attempted to trace a series showing the development of the perithecium of the typical Sphaeriales type from the stroma of the Dothideales through the Pseudosphaerialean genera *Pleospora*, *Pyrenopeziza* and *Leptosphaeria*. He also attempted to trace the development of the ostiole from a pore developed lysigenously to a true ostiole lined with periphyses, and the development of the paraphyses from strands of stroma tissue, connected above and below the developing asci, to true paraphyses of typical structure such as are found in the Sphaeriales. Gaumann (1928) adopted this scheme, and stated that true perithecia are formed by the fungi regarded as higher Pseudosphaeriaceae, and these are therefore truly Sphaeriaceous.

Recently Miller (1928a) has shown that the disagreements between the earlier writers over the nature of the fungi variously attributed to the Sphaeriales and Pseudosphaeriales were due to non-appreciation of the true nature of the perithecial wall in the Sphaeriales. He maintained that the stroma is vegetative tissue which does not arise as the result of sexual stimulus, and that the perithecial wall is "specialised tissue which arises from the archicarp and from the beginning encloses the ascogenous centrum" (p. 194), the asci, paraphyses and periphyses also being produced by the archicarp.

It is clear, therefore, that there can be no transition in the way maintained by Petrak from the Sphaeriales to the Dothideales, since the development of the elements of the ascospore producing fructification is fundamentally different. In the Pseudosphaeriales and Dothideales the apical pore develops lysigenously and the paraphyses are stromatic in origin, while in the true Sphaeriales periphyses grow up from the perithecial wall tissue to form a true ostiole lined by cells of ascogenous origin, and the paraphyses grow from the ascogenous hyphae at the base of the perithecium. Blain (1927) also maintained that in the Dothideales the development of the pore is lysigenous, and there is no perithecial wall. Orton (1924), in an extensive review of literature on the stroma, also came to the conclusion that it is definitely a vegetative structure.

Miller (1928a) has shown that in *Guignardia*, a fungus previously placed in the Sphaeriales, a homogeneous stromatic matrix is formed. In this stroma an archicarp is differentiated, and gives rise to asci which grow at the expense of the stroma, causing its disintegration. He also considered that *Teichospora* belongs to the Dothideales. Nichols (1896) has described in *Teichospora* the development of a solid stromatic body in which the asci develop. In the stromatic Sphaeriales, Wehmeyer (1926), Miller (1928b) and others have shown that a true perithecium wall and ostiole develop from coiled Woronin hyphae.

Miller concluded that the Pseudosphaeriales have no features not in common with the Dothideales, and recommended that they be merged with them, and

their position determined by characters of ascus and spores and ascial hymenium rather than by the thickness of the stroma wall or the number of locules in the stroma as hitherto.

He considered that the Pseudosphaeriales, Perisporiaceae, Coryneliaceae and Dothideaceae are characterized by the absence of a true perithecial wall, and by the asci being borne in locules of a stroma. Since they do not develop true perithecia he believes that they cannot be regarded as Pyrenomycetes.

Following Miller's scheme the Capnodiaceae belong to the Dothideales, since the perfect fruit-body has been shown to develop as a stroma, no perithecial wall being formed.

The Capnodiaceae are not related to the simple Sphaeriales which show the development of antheridia and ascogonia, or to the stromatic Sphaeriales in which the perithecium develops from coiled Woronin hyphae.

It does not appear that there is any close relationship to the Perisporiaceae or Erysiphaceae. In the Erysiphaceae it is well known that a true perithecium is developed after the formation of an ascogonium, with or without an antheridium. In *Meliola* (Perisporiaceae) Graff (1932) has recently shown that a true perithecium wall is formed under a shield-like structure, and that antheridium and ascogonium are produced though no fusion was observed.

Arnaud (1910) considered that the species of the Capnodiaceae showed close affinities with the Sphaeriales and placed *Capnodium salicinum* in the genus *Teichospora*, and *Capnodium (Aithaloderma) citri* in the genus *Pleosphaeria*. Nichols (1896) has shown that *Teichospora* forms a solid stroma, and Arnaud himself (1910) described the early stages of the development of a stroma in *Pleosphaeria citri*. Neither of these genera can therefore be placed in the Sphaeriaceae. In *Teichospora*, Nichols described the formation of an oval uninucleate cell from the parenchymatous tissue of the stroma, and stated that asci appear without fertilization.

The formation of the stroma in *Teichospora* appears to differ markedly from that in the Capnodiaceae in that an almost solid body is formed by the segmentation of a vegetative hypha, and the description of the development of the ascogenous hyphae is not sufficiently detailed to permit of close comparison. The habit of *Teichospora* which grows on dead branches, often partly submerged, also differs from that of *Capnodium*, which is superficial and grows only on the honey-dew excreted by scale insects. For the present, therefore, it seems best that *Teichospora* should not be included in the same genus as *Capnodium*.

Very little is known of the early stages in the development of the ascogenous hyphae in the Dothideales. In *Dothidella ulmi*, the only species which has been investigated in detail, Killian (1920) described the formation of an archicarp of 3-4 cells, each of which becomes 2-3-nucleate. These come into communication by breakdown of walls and fuse in pairs, then entering the ascogenous hyphae. This method of development resembles that of *Capnodium* and *Aithaloderma* more closely than any other described type. The chief difference is the number of nuclei in the cells of the archicarp.

It is impossible to say whether the stroma of the Capnodiaceae is reduced from a multilocular form such as *Dothidella*, or whether the tendency to form bilocular stromata indicates that it is a primitive type of the Dothideales.

Orton (1924) has shown that in *Catacauma* a rudimentary perithecial wall of a few "nurse" cells is formed, which is resorbed by the developing asci. This indicates that the Dothidealean type of fructification may have been derived from

the stromatic Sphaeriales by reduction, rather than that, as Petrak (1923) has attempted to show, evolution should have taken place from the Dothideales to the Sphaeriales. In this case the Capnodiaceae would represent a further stage in reduction of both perithecial wall and stroma.

There does not appear to be sufficient justification for Woronichin's proposed order, Capnodiales, as these fungi show no features which should exclude them from the Dothideales as defined by Miller.

Certain types of elaboration after reduction, so that structures are produced resembling those of different origin found in unrelated fungi, are seen in *Aithaloderma viridis* and *Capnodium*. In the one, a stromatic wall somewhat resembling a perithecial wall is developed within the stroma, and in the other, stroma threads may concentrate under the pore resembling periphyses to some extent.

In consideration of these facts the writer considers that the family Capnodiaceae should be placed in the Dothideales.

The Nomenclature of Capnodium salicinum.

Arnaud (1911) has pointed out that Montagne (1849), in his description of the type of *Capnodium salicinum*, confused the pycnidia and the ascogenous fructifications, both of which produce spores which are very much alike. Montagne's description of the ascogenous fructifications therefore included the shape types of the pycnidia. Later authorities have followed this error, but Tulasne, Kickx and later von Hoehnel (1909) have given revised descriptions which are quite adequate. There is no reason, therefore, for placing the species of the genus *Capnodium* in other later-formed genera as Arnaud has done, especially since, as has been shown in this paper, it is doubtful whether the relation to *Teichospora* is a close one. Further investigations on the life history of *Pleosphaeria* are necessary before the relationship of *Aithaloderma citri* to this genus can be proved.

Summary.

An examination has been made of the life histories of four species of *Capnodium* and *Aithaloderma*, members of the Capnodiaceae.

In all species the mycelium consists of uninucleate cells, and the hyphae branch and anastomose at wide angles.

In *Capnodium* the pycnidia are compound meristogenous in origin, and vertically elongated when mature. The ascogenous fructification arises as a stroma which develops from the division and subsequent growth of several adjoining cells of a hypha, and is composed of loosely-woven threads with an outer dark wall layer and a thin-walled core-tissue. The archicarp arises from a vegetative hypha at the base of the core, and consists of a number of cells. The archicarp becomes multinucleate, probably by the resorption of the walls between the cells. The nuclei associate and probably fuse in pairs. Ascogenous hyphae bud out and branch through the base of the core, giving rise to asci which grow vertically up through the core-tissue, resorbing it. No fusions have been observed in the young ascus. An apical pore develops lysigenously, and stroma hyphae grow up under it simulating periphyses.

In *Aithaloderma ferruginea* the pycnidia are compound meristogenous in origin, and are rather flat when mature. The stroma develops (1) by growth in thickness under a meristogenously formed disc, (2) radially by growth around the edges, and (3) by a certain amount of upward growth in the young stage,

as in *Capnodium*. The archicarp arises at the base as in *Capnodium*, and nuclear fusions probably take place. Ascogenous hyphae grow out across the base of the stroma, giving rise to asci as in *Capnodium*. The apical pore is developed lysigenously.

In *Aithaloderma viridis*, increase in thickness of the ascogenous stroma takes place exclusively beneath a radially growing disc. A compact wall of stromatic tissue is developed round the young asci distinct from the more loosely woven stroma tissue round it and resembles a perithecial wall.

It is concluded that the Capnodiaceae as represented by *Capnodium* and *Aithaloderma* should be placed in the order Dothideales.

In conclusion the writer desires to thank Professor T. G. B. Osborn and Professor J. McLuckie for helpful criticism and advice, and Miss J. Vickery and Mr. A. Burges for confirming observations.

Literature Cited.

- ARNAUD, G., 1910.—Contribution à l'étude des Fumigines. 1. *Ann. Ecole nationale Agric. Montpellier*, Sér. 2, Tome ix (4), pp. 239-277.
- , 1911.—Contribution à l'étude des Fumigines. 2. *Ibid.*, Tome x (3/4), pp. 211-330.
- BLAIN, Walter Leroy, 1927.—Comparative Morphology of Dothideaceous and Kindred Stromata. *Mycologia*, 19 (1), pp. 1-20.
- GAUMANN, E. A., 1928.—Comparative Morphology of the Fungi. Translated by C. W. Dodge. New York.
- GRAF, Paul W., 1932.—The Morphological and Cytological Development of *Meliola circumans*. *Bull. Torrey Bot. Club*, 59 (5), pp. 241-266.
- HOEHNEL, F. VON, 1907.—Fragmente zur Mykologie III. *Mitt. Nr. 92-155. Sitz. K. Acad. Wiss., Math.-Nat. Kl. Wien*, 116, pp. 83-162.
- , 1909.—Fragmente zur Mykologie. VIII. *Mitt. Nr. 379. Ueber Limacinula samoensis* von H. *Ibid.*, 118, pp. 1193-1201.
- , 1910.—Fragmente zur Mykologie. XII. *Mitt. Nr. 611. Ibid.*, 119, pp. 913-919.
- , 1918.—Fragmente zur Mykologie. XXI. *Mitt. Nr. 1089. Ueber die Capnodiaceen und Coccodiniaceen. Ibid.*, 127 (1), pp. 386-389.
- KEMPTON, F. E., 1919.—Origin and Development of the Pycnidium. *Bot. Gazette*, 68 (4), pp. 233-261.
- KILLIAN, C., 1920.—Le Développement du *Dothidella ulmi*. *Rev. Gén. Botanique*, 32, pp. 534-551.
- MILLER, Julian H., 1928a.—Biological Studies in the Sphaeriales. 1. *Mycologia*, 20 (4), pp. 187-213.
- , 1928b.—Biological Studies in the Sphaeriales. 2. *Mycologia*, 20 (6), pp. 305-339.
- MONTAGNE, C., 1849.—De Capnodio, nov. gen. *Ann. Sci. Nat.*, Sér. 3, Tome ii.
- NICHOLS, Mary A., 1896.—The Morphology and Development of Certain Pyrenomycetous Fungi. *Bot. Gazette*, 22, pp. 301-328.
- ORTON, C. R., 1924.—Studies in the Morphology of the Ascomycetes. 1. *Mycologia*, xvi (2), pp. 49-95.
- PETRAK, F., 1923.—Mykologische Notizen. V. Nr. 200. Ueber die Pseudosphaeriaceen v.H. und ihre Bedeutung für die spezielle Systematik der Pyrenomycetous. *Annales Mycologici*, xxi (1/2), pp. 1-69.
- , 1929.—Mykologische Notizen. Nr. 670. Ueber einige Chaetothyriaceen—Gattungen. *Ibid.*, xxvii, p. 380.
- THEISSEN, F., and SYDOW, H., 1917.—Synoptische Tafeln. *Ann. Mycol.*, 15, pp. 389-491.
- , 1918.—Vorentwürfe zu den Pseudosphaeriales. *Ibid.*, 16, pp. 1-34.
- WEHMEYER, L. E., 1926.—A Biological and Phylogenetic Study of the Stromatic Sphaeriales. *Amer. Journ. Bot.*, xliii (10), pp. 575-645.
- WORONICHIN, N. N., 1925.—Über die Capnodiaceen. *Annales Mycologici*, 23, pp. 174-178.